

# A trans-Atlantic examination of haddock Melanogrammus aeglefinus food habits

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TITLE: A Trans-Atlantic Examination of Haddock (*Melanogrammus aeglefinus*) Food Habits

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ABSTRACT

Haddock (*Melanogrammus aeglefinus*) is a commercially and ecologically important gadoid in the food webs and economies of regional ecosystems across the North Atlantic. *Melanogrammus aeglefinus* is reported to be primarily piscivorous in some cases and primarily an echinoderm feeder in others. Often, the species exhibits ontogenetic dietary shifts, focusing on a specific prey at small sizes and on different prey at larger sizes. Here we explore and contrast the food habits of *M. aeglefinus* across multiple northeastern and northwestern Atlantic ecosystems, using databases that span multiple decades. The results show that, among all ecosystems, echinoderms are a consistent part of *M. aeglefinus* diet, but patterns do emerge regarding where and when *M. aeglefinus* primarily eat fishes versus echinoderms. *Melanogrammus aeglefinus* does not regularly exhibit the increase in piscivory with ontogeny that other gadoids often show, in several ecosystems there is a lower occurrence of piscivory. There is an apparent inverse relationship between the consumption of fishes and echinoderms in *M. aeglefinus* over time, where certain years show high levels of one prey item and low levels of another. We view this apparent binary choice as part of a gradient of prey options, contingent upon a suite of factors external to *M. aeglefinus* dynamics. We discuss the energetic consequences of this prey choice, noting that in some instances it may not be a choice at all.

KEY WORDS: haddock, prey choice, echinoderms, piscivory, ecosystem-based fisheries management

47 INTRODUCTION

48

49 An integral part of managing commercial fish stocks from an Ecosystems-Based Fisheries
50 Management (EBFM) perspective is understanding trophic linkages and the nature of feeding
51 choices in target species (Pauly *et al.*, 1998; Link *et al.*, 2002). For predatory species, prey
52 selection defines their ecological role and offers insight into how these species can and should be
53 managed (Greenstreet *et al.*, 1997; Link *et al.*, 2009; Branch *et al.*, 2010). For historically
54 harvested fish stocks, such as gadoids and pleuronectiformes in the North Atlantic, it is important
55 to understand their functional roles and what ecological buffers exist (in terms of functional
56 redundancies, where multiple species contribute in equal ways to ecosystem function) against
57 direct and indirect effects of overexploitation (Bellwood *et al.*, 2003; Link, 2007). In the case of
58 geographically-widespread, opportunistic predators, populations of the same species can develop
59 differing dietary strategies and specializations. This has been well documented in marine
60 mammals where species such as harbour seals *Phoca vitulina* and killer whales *Orcinus orca*
61 exhibit a variety of prey specializations between their geographically widespread populations
62 even though they are able to eat a substantial range of prey (Ford *et al.*, 1998, 2010; Tollit *et al.*,
63 1998). Fewer such comparisons are made between fish populations, but examinations of fisheries
64 literature indicates that dietary specializations occur in opportunistic fish predators. For example,
65 the spiny dogfish *Squalus acanthias* is a widespread commercial fish that appears to consume
66 proportionately more benthic invertebrates in New Zealand (Hanchet, 1991), teleost fishes in the
67 North Atlantic (Holden, 1966; Link *et al.*, 2002) and large proportions of Euphausiids in the
68 Eastern Pacific (Jones & Geen, 1977; Tanasichuk *et al.*, 1991). This can have strong
69 implications on how target species are managed in different parts of the world as local

abundances of preferred prey can dictate the stock size of the predator and subsequent functional redundancies may differ from place to place (ecosystem to ecosystem).

Haddock *Melanogrammus aeglefinus* is an important species in the North Atlantic, with a long history of commercial exploitation (Jensen, 1965; Bergstad *et al.*, 1987; Pope & Macer, 1996; Hedger *et al.*, 2004). *Melanogrammus aeglefinus* is a widespread species with fisheries in the east coast of North America and in many parts of northern Europe and the British Isles (Aleev, 1944; Jensen, 1965; Albert, 1994; Jiang & Jørgensen, 1996; Temming *et al.*, 2004; Bogstad *et al.*, 2013). Juvenile *M. aeglefinus* transition after 3-5 months from living in the upper reaches of the water column to living on muddy, sandy or gravel substrate (Platt *et al.*, 2003; Sell & Kröncke, 2013). As demersal fish, they spend their adult life in close association with benthic habitat. Like other gadoids, they are opportunistic, higher-trophic-level feeders and prey on a variety of fishes and invertebrates (Schückel *et al.*, 2010; Smith & Link, 2010). Although *M. aeglefinus* is an abundant species in many ecosystems and its feeding behaviour is extensively studied in specific locales (Tseeb, 1964; Sonina, 1969; Dolgov *et al.*, 2007), overviews about its diet or how its diet may change throughout its life history or across its geographic range have not been executed comparatively.

Echinoderms have been relatively well studied in marine ecology, primarily as consumers. Notable examples are crown-of thorns *Acanthaster planci* decimating corals in the Indo-Pacific (Moran *et al.*, 1992; Vogler *et al.*, 2008), seastars *Pisaster ochraceus* as a keystone predator on North Pacific intertidal communities (Paine, 1966, 1969) and sea urchins *Strongylocentrotus droebachiensis* denuding temperate areas entirely of macrophytes (Watanabe & Harrold, 1991;

93 Gagnon *et al.*, 2004; Lauzon-Guay & Scheibling, 2007). However, outside of the sea otter-
94 urchin-macrophyte feeding dynamic (Estes & Palmisano, 1974; Dayton, 1975), studies of
95 predation on echinoderms seldom occur (but see Pinnegar *et al.*, 2000; Schückel *et al.*, 2010).
96 Furthermore, the trophic role of echinoderms in deeper, subtidal communities is undervalued
97 commercially as well as ecologically and not well studied compared to the role of fish prey,
98 particularly in the northern Atlantic.
99
100 A unique aspect of *M. aeglefinus* feeding is that echinoderms can make up a significant part
101 of their diet in the Northwestern Atlantic (Mahon & Neilson, 1987; Link, 2004; Shackell *et al.*,
102 2010; Smith & Link, 2010). This is rare among gadoids and from an energetic perspective would
103 appear to be counterintuitive (Dauvin & Joncourt, 1989). With the exception of sea cucumbers,
104 echinoderms are mainly composed of thick, calcareous exoskeletons that are only slowly
105 digested by most fishes and contain less energy per gram than other invertebrate diets items
106 including worms, gastropods, bivalves and crustaceans (Steimle & Terranova, 1980). Survey
107 observations of fish stomach contents in the Northwest Atlantic has shown that several species
108 consume echinoderms at some point in their life histories (Link, 2004; Smith & Link, 2010;
109 Bundy *et al.*, 2011). The fact that commercially important fishes, like *M. aeglefinus*, choose to
110 eat echinoderms is rarely addressed in fisheries management and ecosystem modelling even
111 though echinoderms appear to play a large role in regulating energy flow in marine food webs
112 (Steimle & Terranova, 1980; Zamarro, 1992).
113
114 What is unclear is the level of consistency across *M. aeglefinus* populations throughout their
115 range in consuming echinoderms as a significant food source. There are indications that the diet

of *M. aeglefinus* differs between areas and time periods. As a consequence, the functional redundancies to *M. aeglefinus* remain unknown. This study aims to examine the diet similarities of *M. aeglefinus* populations throughout their distributional range, at different stages during their life history and across several decades. This is an important step in understanding the dynamics in feeding ecology of *M. aeglefinus* and the role of echinoderms in benthic ecosystems.

## MATERIALS AND METHODS

### *Study areas and data collection*

*M. aeglefinus* stomachs were collected from nine ecosystems in the North Atlantic (Figure 1). In the Gulf of Maine, Georges Bank, Scotian Shelf, Rockall Bank, North Sea and Barents Sea diet composition was assessed as the weight of the diet item relative to the total weight of the stomach contents. In the Celtic Sea, Irish Sea and Spitzbergen (Svalbard), frequency of occurrence (FO; the number of stomachs containing the diet item relative to the total number of stomachs) was used to assess the diet (Hyslop E. J., 1980; Ahlbeck *et al.*, 2012). The sampling primarily occurred from the 1970s to present, but extended to earlier decades for some regions (Table 1).

Stomach contents were collected from length-stratified samples during fishery-independent and fishery-dependent surveys, and prey were quantified by weight or number depending on where and what type sampling occurred (Table I). Where possible, prey items were

identified to species level; however, due to varying levels of digestion prey were often identified to genus, class or family levels (Smith & Link, 2010; Bundy *et al.*, 2011; Cook & Bundy, 2012).

*Data analysis*

Data were parsed to include only the dominant prey of *M. aeglefinus* diet. Because they have been described elsewhere in detail for given ecosystems (Table I), non-echinoderm invertebrates (worms, gastropods, bivalves and crustaceans) were not considered in the analyses. As each ecosystem may contain a different selection of prey species and given the aims of this study, we grouped prey according to rough taxonomic classification of echinoderm, fish, or other prey item. To determine if *M. aeglefinus* undergo similar ontogenetic shifts in diet composition across regions, we also grouped *M. aeglefinus* into the following size groups: 10-29, 30-49, and > 50 cm where data were available. These sizes are consistent with observed major ontogenetic shifts in diet(Link & Garrison, 2002a). Where time series data was available (Georges Bank, Gulf of Maine, US Scotian Shelf and Barents Sea), *M. aeglefinus* diet was plotted in 5 year blocks to examine consistency in food choice over time.

Given that the diet of *M. aeglefinus* was recorded differently between ecosystems, Kendall's tau (Fredricks & Nelsen, 2007) was used to examine the non-parametric, rank-order relationship between the proportion of echinoderm and fish in the diet of *M. aeglefinus* in differing ecosystems. This statistical method is the non-parametric equivalent of measures of association or correlation .This analysis determined if there was any consistent and significant association between the amount of fishes and echinoderms in the diet of *M. aeglefinus* for all

ecosystems examined. Within ecosystem differences between echinoderms and fishes in *M. aeglefinus* diet were determined using Chi-square analysis. To explore and test for relationships within ecosystems of *M. aeglefinus* diet between size classes, Chi-square analysis of the proportion of each diet item in the stomachs of fish across size classes was used. To examine trends in prey selection of *M. aeglefinus* at each ecosystem over time, a generalized linear model was used with percent of the diet item as the dependent variable and time as the independent variable. This determined if *M. aeglefinus* showed general shifts in their prey selection over time. At each 5 year block within each ecosystem, a Chi-square analysis was performed to determine significant differences between the percentage of echinoderms and fishes in *M. aeglefinus* diet and reveal any changes in the feeding pattern of *M. aeglefinus* over time.

## RESULTS

There was no significant relationship of echinoderms and fishes in the diet of *M. aeglefinus* that could be applied to all ecosystems according to the Kendall's tau analysis (Figure 2; $\tau = 0.33$, Z-score = 1.25, $p = 0.21$). The North Sea and Rockall Bank populations of *M. aeglefinus* showed significantly higher piscivory, while all other ecosystems showed significantly higher echinoderms consumed or else no dominant prey (Table II).

Differing patterns of ontogenetic shifts towards piscivory were apparent in *M. aeglefinus* among ecosystems based on size class data (Figure 3). In several ecosystems there was a significantly lower occurrence of piscivory (i.e. eggs and larvae) with increasing size (Georges Bank: $X^2 = 30.52$, df = 2, $p = <0.001$; Gulf of Maine: $X^2 = 15.91$, df = 2, $p = <0.001$). In the

North Sea and Rockall Bank there was a higher occurrence of piscivory (i.e. small pelagic fishes) with increasing size class ($X^2$ = 38.34, 23.90, df = 2, 2, $p$ < 0.001, <0.001, respectively), but the proportion of echinoderms in the diet of *M. aeglefinus* remained constant. Through their life history, *M. aeglefinus* ate a large proportion of echinoderms in most ecosystems. Echinoderms were a proportionately consistent component of *M. aeglefinus* diet throughout their life cycle except in the Gulf of Maine and Scotian Shelf, where echinoderms increased in frequency with increasing size ($X^2$ = 22.29, 17.82, df = 2, 2, $p$ <0.001, <0.001, respectively ).

There was no consistent temporal shift in the diet of *M. aeglefinus* in either echinoderms or fishes within ecosystems ($F_{1,4}$ = 0.18, $p$ = 0.95). Long-term stomach content data indicated that echinoderms were consistently a part of *M. aeglefinus* diet over time, but neither diet item exhibited any positive or negative linear trend, indicating that there was no shift in diet related to an external pressure (i.e. environment or habitat). Despite the lack of trend, the Chi-square analyses indicated that there were significant differences in the consumption of echinoderms and fishes by *M. aeglefinus* within time periods (Table III). There appeared to be an inverse relationship between the consumption of fishes and echinoderms by *M. aeglefinus* over time. Periods of high and low fish consumption by *M. aeglefinus* coincided with respective periods of low and high echinoderm consumption (Figure 4). During the late 1980s and early 2000s there appeared to be peaks in echinoderm consumption by *M. aeglefinus*.

## DISCUSSION

It is unusual for a gadoid species to consistently maintain a high proportion of benthic invertebrates in its diet throughout its life history. Most gadoids are known to be opportunistic:

Atlantic cod *Gadus morhua* being a generalist feeder, saithe *Pollachius virens* and some hake species consuming more of a pelagic diet (Smith & Link, 2010). *Gadus morhua* have shown a clear ontogenetic shift in diet, with smaller *G. morhua* feeding more on benthic prey and larger *G. morhua* showing a strong shift towards piscivory (Link & Garrison, 2002b; Smith *et al.*, 2007; Rowlands *et al.*, 2008). In contrast, *M. aeglefinus* exhibit no ontogenetic shift towards piscivory with the exception of the North Sea and Rockall Bank, where echinoderms still occur in their diets throughout their lives. This difference in ontogenetic diet shift between *M. aeglefinus* and *G. morhua* can be explained by the smaller gape size and body size of *M. aeglefinus* that are not able to eat as many larger prey fish compared to *G. morhua* (Løkkeborg *et al.*, 1989).

*M. aeglefinus* consistently consume echinoderms across the range of environmental conditions examined. In ecosystems where *M. aeglefinus* appear to be more piscivorous or predominantly eat a combination of other invertebrates, echinoderms still make up at least 10% of their diet. Since the early 2000s *M. aeglefinus* stocks have experienced an increase in abundance in all regions studied with the exception of the Scotian Shelf and, thus, do not appear to be suffering from reduced productivity due to their reliance on low-nutrient food sources (Brodziak *et al.*, 2008; Bogstad *et al.*, 2013; Pecuchet *et al.*, 2014). Eating food of high calcium carbonate and low energy may have developed in *M. aeglefinus* to reduce competition with other gadoids by obtaining a consistent, albeit low-energy food source.

While it may not seem like a successful strategy to consume large proportions of echinoderms due to their low nutritional value compared to prey fish, their relatively high

abundances and relatively low defenses (slow moving) make them a very accessible prey to *M. aeglefinus*. Echinoderms in the northwestern Atlantic make up a large proportion of the biomass in benthic habitats (up to 500 g $m^{-2}$ and up to 90% of the total grab sample) with sand dollars *Echinarachinius parma* in shallower regions and brittlestars *Amphioplus* spp. and sea cucumbers dominating deeper areas of Georges Bank and the Gulf of Maine basins (Steimle, 1990). In Atlantic Canada, echinoderms at times have made up to 35% of the total cal $m^{-2}$ of benthic habitat even though they are relatively low in energy content compared to other invertebrate phyla (Brawn *et al.*, 1968). In the North Sea, the brittlestar *Amphiura filiformis* dominates the benthic system and lives in densities up to 2250 indv $m^{-2}$ (Skold *et al.*, 1994; Wood *et al.*, 2009), and other important species include *Echinocyamus pusillus*, *Ophiura albida*, *Ophiura affinis*) and *Echinocardium cordatum* that are also common components of the benthos . These high abundances of echinoderms in benthic communities support the hypothesis that *M. aeglefinus* exhibit ambient feeding in some regions to perhaps sustain the populations while supplementing their diet with other prey.

In this study the diet of *M. aeglefinus*, consistently include echinoderms across ecosystems and over time, even in regions where the dominant prey is fish. This indicates that echinoderms are an important food source throughout their distribution. While there does not appear to be long-term, multi-decadal shifts in the diet of *M. aeglefinus*, there is an indication of shorter-term changes in *M. aeglefinus* feeding habits (Figure 4). At five year intervals in Georges Bank, Gulf of Maine, Scotian Shelf and Barents Sea there is evidence of an inverse relationship between the contribution of echinoderms and fish prey to the diet of *M. aeglefinus* (Antipova *et al.*, 1980). Foraging fish are known to be able to alter their behaviour in response to

253 variations in food availability and the threat of competition (Dill, 1983). *Melanogrammus*
254 *aeglefinus* likely consume lower quality food choices when faced with adversity in acquiring a
255 preferred resource (Vinyard, 1980; McNamara & Houston, 1987). Feeding on echinoderms could
256 be a strategy for *M. aeglefinus* to maintain constant energy levels during periods of low prey fish
257 abundance and high competition with other gadoids that may occur on a multi-annual cycle
258 (Temming *et al.*, 2004). However, intra-annual abundances for all prey items of *M. aeglefinus*
259 from the ecosystems surveyed in this study were not examined and it would be a useful avenue
260 for future research to measure selectivity across time in all of these populations.
261
262 An opportunistic feeding mode for *M. aeglefinus* has been demonstrated in several earlier
263 studies (Mattson, 1992; Schückel *et al.*, 2010) and current observations from the different
264 ecosystems reveals that high amounts of fish in the diet of larger North Sea *M. aeglefinus* is
265 likely to be a consequence of prey availability rather than an ontogenetic shift (i.e. the high
266 abundance of sandeels *Ammodytes* spp.). This is supported by observations on Dogger Bank in
267 the North Sea, where Sell and Kröncke (2013) found the distribution of *M. aeglefinus* to be more
268 strongly correlated with abiotic habitat parameters (depth, temperature, sediment composition)
269 than with biotic factors, including the availability of potential mud dwelling prey. It has also
270 been shown that *M. aeglefinus* adapt their diets based on prey availability due to benthic
271 disturbance from fishing gear with less benthos and slightly more fish consumed in disturbed
272 habitats (Smith *et al.*, 2013).
273
274 There is some indication that echinoderms have higher nutrition and energy content than
275 expected, but past studies have shown that the caloric content of fish to be higher than

276 echinoderms. Brawn et al. (1968) found that prey fish contained 2-3 times more cal $g^{-1}$ than
277 echinoderms in St. Margaret's Bay in Nova Scotia, Canada. Other studies have found lower
278 energy content in seastars and brittlestars compared to fish (19.10 kJ $g^{-1}$ for echinoderms and
279 22.96-24.22 kJ $g^{-1}$ for fish; ash-free dried weight), while sea urchins had a higher energy content
280 (25.82 kJ $g^{-1}$; ash-free dried weight) than both demersal or pelagic fishes (Steimle & Terranova,
281 1980; Packer *et al.*, 1994). Inconsistencies in the values of energy contents drawn from these
282 studies may be due to the different species contributing to the sample groups. There may also be
283 a seasonal element to the appeal of echinoderms as *M. aeglefinus* prey. When echinoderms are
284 gravid they are more nutritionally valuable and contain a higher lipid and protein content.
285 Steimle and Terranova (1980) found that the energy content in *E. parma* doubled during autumn
286 spawning periods compared to spring values. Certain conditions in timing and availability may
287 make echinoderms a logical food choice for *M. aeglefinus*.
288
289 There is some evidence that hard shelled invertebrates, such as echinoderms and bivalves,
290 digest more slowly and less efficiently than other, soft-tissue prey such as fishes and polychaetes
291 (MacDonald *et al.*, 1982; Tibbetts *et al.*, 2004; Jaworski & Ragnarsson, 2006). Preliminary
292 calculations indicate that the digestibility of hard shelled invertebrates are only approximately
293 10% less than that of soft bodied prey such as fish and polychaetes in gadoid diets, and
294 respective evacuation rates could be on the order of 1-2 times slower (MacDonald *et al.*, 1982;
295 Tibbetts *et al.*, 2006). If this is the case, the relative importance of echinoderms in the diet of *M.*
296 *aeglefinus* could potentially be amplified by a similar factor. If, however, the percent diet
297 composition of echinoderms in the diet of *M. aeglefinus* is lower, the fact remains that
298 echinoderms still remain a notable, consistent and regular component of the diet of *M.*

299 *aeglefinus*. In contrast, there is evidence that the shells in echinoderms may actually promote
300 more efficient digestion in predatory fish. Mattson (1992) indicates that the calcareous shell of
301 echinoderms act as a grinding element and can enhance digestion as well as ingestion. This
302 increased maceration may compensate for the low nutritional value inherent in echinoderm prey
303 and could ultimately improve the digestion of all hard shelled organism in *M. aeglefinus* diet.
304
305 The implications of understanding the diets of target fish species span far beyond just
306 knowing what they are eating. Assessing food habits in fishes, particularly in opportunistic
307 feeders, can give insight into habitats and prey species distributions that are difficult to survey
308 (Link, 2004; Cook & Bundy, 2012). In determining that *M. aeglefinus* consume large proportions
309 of echinoderms in many regions, this study has identified an important link between the benthos
310 and harvested fish. This is a mechanism that is rarely considered in management decisions and
311 implies that impacts to the benthic habitat in certain regions will likely affect *M. aeglefinus* more
312 than other harvested gadoid species. From an EBFM perspective, the functional redundancies of
313 *M. aeglefinus* lie alongside other echinoderm consumers such as American plaice
314 *Hippoglossoides platessoides* and ocean pout *Macrozoarces americanus* rather than species of
315 the same family group (Zamarro, 1992; Packer *et al.*, 1994; Link, 2007).
316
317 While traditional conservation strategies, such as fisheries closures, are not always
318 effective at increasing target fish stocks (Fisher & Frank, 2002; Kelly *et al.*, 2006), *M. aeglefinus*
319 have historically responded well to these management options (Brodziak *et al.*, 2008). In the
320 mid-1990s, *M. aeglefinus* stocks in the northwest Atlantic were the lowest on record (Hutchings,
321 2000). After strict closures as a response by the declining stock status, *M. aeglefinus* stocks

increased dramatically (Murawski *et al.*, 2000; Brodziak *et al.*, 2008). *Melanogrammus aeglefinus* are also known to have a restricted daily ambit compared to other gadoids, indicating a strong association with local habitats (Perry & Smith, 1994; Fogarty *et al.*, 2001). Reduced impacts to the benthic habitat compounded with the high proportion of echinoderms in *M. aeglefinus* diet, in part, explain why *M. aeglefinus* stocks have successfully responded to fisheries closures and MPAs (Smith *et al.*, 2013). In areas where *M. aeglefinus* exhibited a high frequency of piscivory, such as the North Sea, fisheries closures did not improve their abundances nearly as much (FSBI, 2001; Fisher & Frank, 2002) . These differences in feeding habits between populations can complicate management efforts because species may not respond the same way in all regions of their distributional range. Thus, conservation methods need to take into account the biology of the ecosystem as well as species-specific life histories to ensure positive and efficient management outcomes.

The importance of the benthic habitat to harvested fish is becoming increasingly apparent. The interconnectedness and complexity of food webs is an important consideration in sustainable fisheries management (Pauly *et al.*, 1998; Link, 2011; Cook & Bundy, 2012; Link & Auster, 2013). To complicate our understanding of trophic webs in fisheries even further, comparative studies such as this one are revealing that populations of the same fish species can interact with their local habitat differently between regions. This emphasizes the need for ecosystem-level management that will improve the resiliency and long-term economic viability of harvested fish throughout their distributions.

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576

577 Table I. Data collection methods and sources. Frequency of occurrence was measured as the number of each diet item relative to the
578 total number of stomachs in percent. Diet composition was measured as the weight of the diet items relative to the total weight of *M.*
579 *aeglefinus* stomachs in percent.

| Ecosystem | Time of sampling | Type of data collected | *M. aeglefinus* stomachs sampled (#) | Collection method | Source |
|---|---|---|---|---|---|
| Gulf of Maine | 1973-1982, 1984-2011 | Diet composition | 3629 | Data compiled from Northeast Fisheries Science Center surveys through random stratified bottom trawl surveys. | (Northeast Fisheries Science Center (NEFSC), 1988; Smith & Link, 2010) |
| Georges Bank | 1973-1982, 1984-1992, 1994-2011 | Diet composition | 5825 | Data compiled from Northeast Fisheries Science Center surveys through random stratified bottom trawl surveys. | (Northeast Fisheries Science Center (NEFSC), 1988, 1998; Smith & Link, 2010) |
| Scotian Shelf | 1995-2009 | Diet composition | 2690 | Data compiled from Department of Fisheries and Oceans trawl surveys. | (Cook & Bundy, 2010, 2012; Bundy *et al.*, 2011) |
| North Sea | 1981, 1991 | Diet composition | 4452 | Data collected during the quarterly International Bottom Trawl Surveys of the North Sea | (International Council for the Exploration of the Seas (ICES), 1989, 1997, 2010) |
| Rockall Bank | 2004-2007, 2009-2010 | Diet composition | 3746 | Data compiled from the Polar Research Institute of Marine Fisheries and Oceanography. | (Antipova *et al.*, 1980) |
| Barents Sea | 1984-1991, 1993-2011 | Diet composition | 11064 | Data compiled by the Institute of Marine Research and the Polar Research Institute of Marine Fisheries and Oceanography. | (Antipova *et al.*, 1980; Dolgov *et al.*, 2007) |
| Irish Sea | 1894, 1981-1983, 2008, 2010 | Frequency of occurrence | 653 | Data compiled from the Centre for Environment, Fisheries and Aquaculture Science. | (Pinnegar, 2014) |
| Celtic Sea | 1977, 1978, 1981-1988, 1991-1993 | Frequency of occurrence | 971 | Data compiled from the Centre for Environment, Fisheries and Aquaculture Science. | (Pinnegar, 2014) |
| Spitzbergen | 1930, 1936, 1937, 1949, 1950, 1954, 1964 | Frequency of occurrence | 735 | Data compiled from the Centre for Environment, Fisheries and Aquaculture Science. | (Pinnegar, 2014) |

Table II. Results of the Chi-square analysis examining the relationship between echinoderms and fish in *M. aeglefinus* diet within each ecosystem. Bold numbers indicate significant differences.

| Ecosystem | $X^2$ | *p*-value | Dominant prey |
|---|---|---|---|
| Gulf of Maine | 3.79 | 0.05 | None |
| Georges Bank | 0.12 | 0.73 | None |
| Scotian Shelf | 2.80 | 0.09 | None |
| **North Sea** | **6.92** | **< 0.01** | **Fish** |
| **Rockall Bank** | **22.11** | **< 0.01** | **Fish** |
| Barents Sea | 0.02 | 0.89 | None |
| Irish Sea | 3.77 | 0.05 | None |
| **Celtic Sea** | **22.54** | **< 0.01** | **Echinoderms** |
| **Spitzbergen** | **43.67** | **< 0.01** | **Echinoderms** |

590 Table III. Results of the Chi-square analysis (p-values) examining the relationship between echinoderms and fish in *M. aeglefinus* diet

591 at each five year block within ecosystems. Bold numbers indicate significant differences.

| Year | Georges Bank | Gulf of Maine | Scotian Shelf | Barents Sea |
|---|---|---|---|---|
| 1975 | **< 0.01** | **< 0.01** | | |
| 1980 | **< 0.01** | **< 0.01** | | |
| 1985 | **< 0.01** | **< 0.01** | | **0.03** |
| 1990 | **< 0.01** | **< 0.01** | | 0.90 |
| 1995 | 0.08 | **< 0.01** | | **< 0.01** |
| 2000 | **< 0.01** | **< 0.01** | **< 0.01** | 0.85 |
| 2005 | **< 0.01** | 0.82 | **< 0.01** | 0.09 |
| 2010 | 0.29 | 0.11 | **< 0.01** | 0.10 |
| 2015 | 0.56 | 0.71 | | 0.59 |

FIGURE CAPTIONS

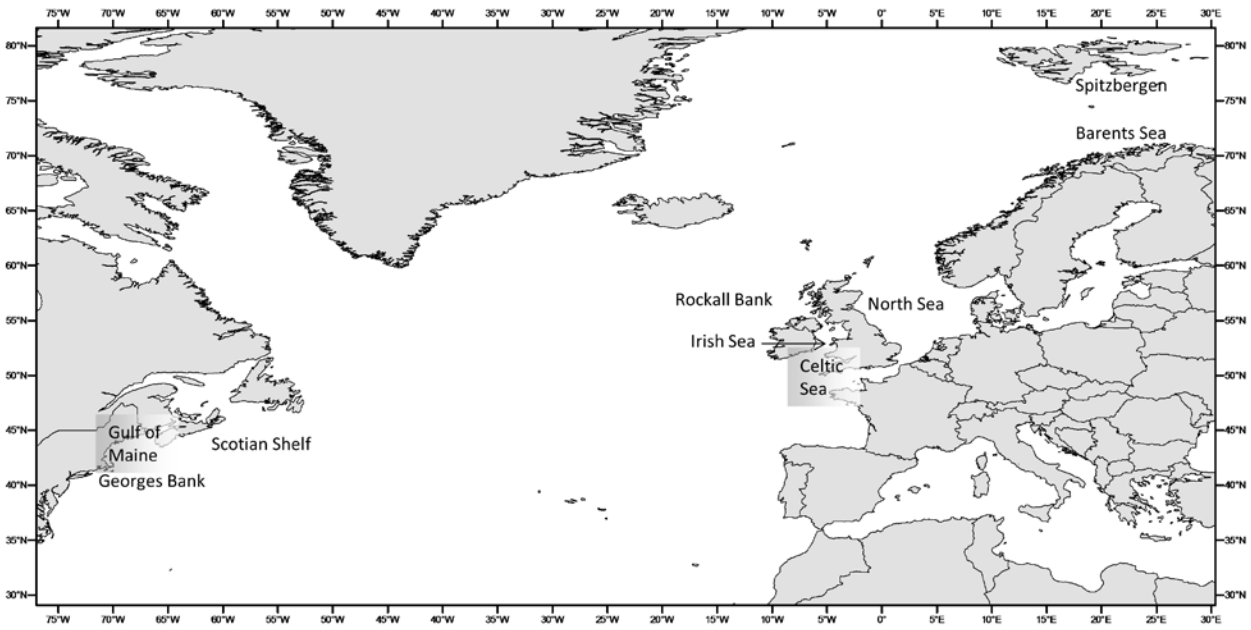
Figure 1. Map of different ecosystems sampled.

Figure 2. Percent contribution of echinoderms and fish to *M. aeglefinus* from different ecosystems. Diet from Celtic Sea, Irish Sea and Spitzbergen were measured in frequency of occurrence (number of stomachs containing the diet item relative to the total number of stomachs), diet from the Barents Sea, North Sea, Rockall Bank, Scotian Shelf, Georges Bank and Gulf of Maine was measured in diet composition (weight of the diet items relative to the total weight of *M. aeglefinus* stomachs in percent).

Figure 3. Percent contribution of echinoderms and fish to the diet of different size classes (cm) of *M. aeglefinus* in different ecosystems where size class data was available.

Figure 4. Percent contribution of echinoderm (grey dotted line) and fish (black solid line) over time (year) in different ecosystems where time series data was available.

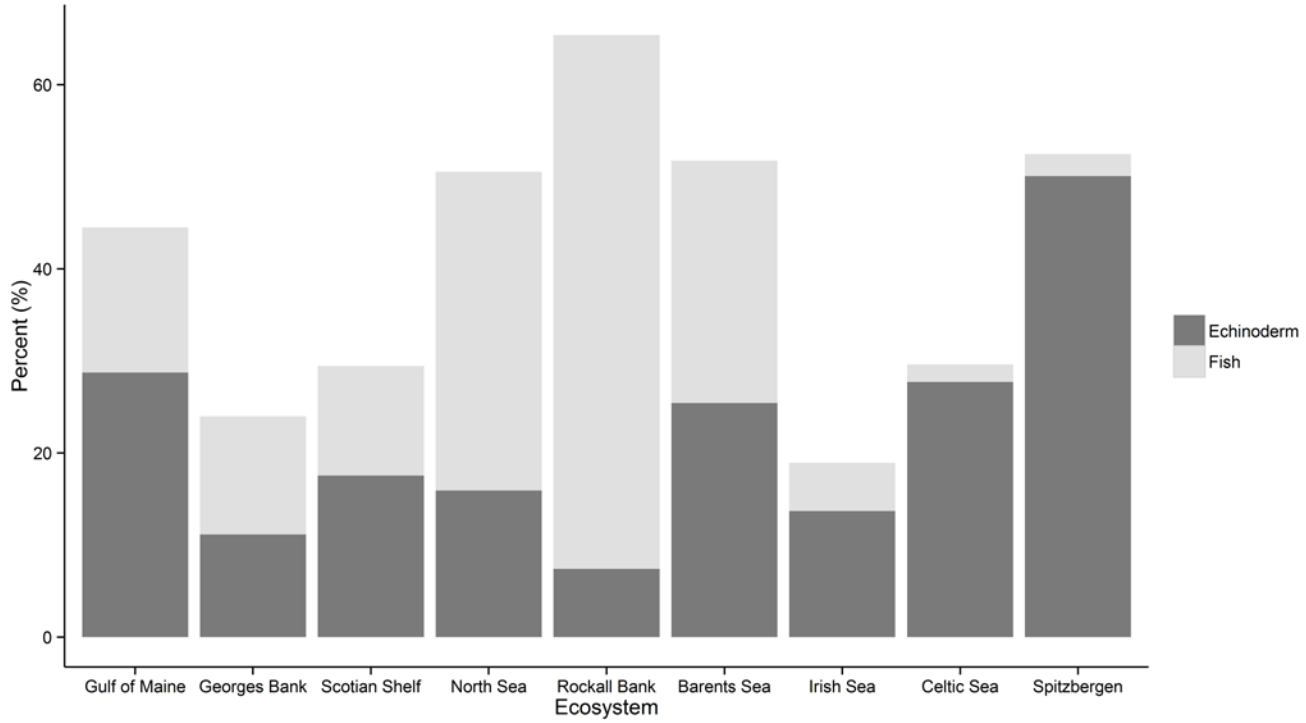
615 FIGURES




616

617 Figure 1. Map of different ecosystems sampled.

618




619

620 Figure 2. Diet of *M. aeglefinus* in different ecosystems.

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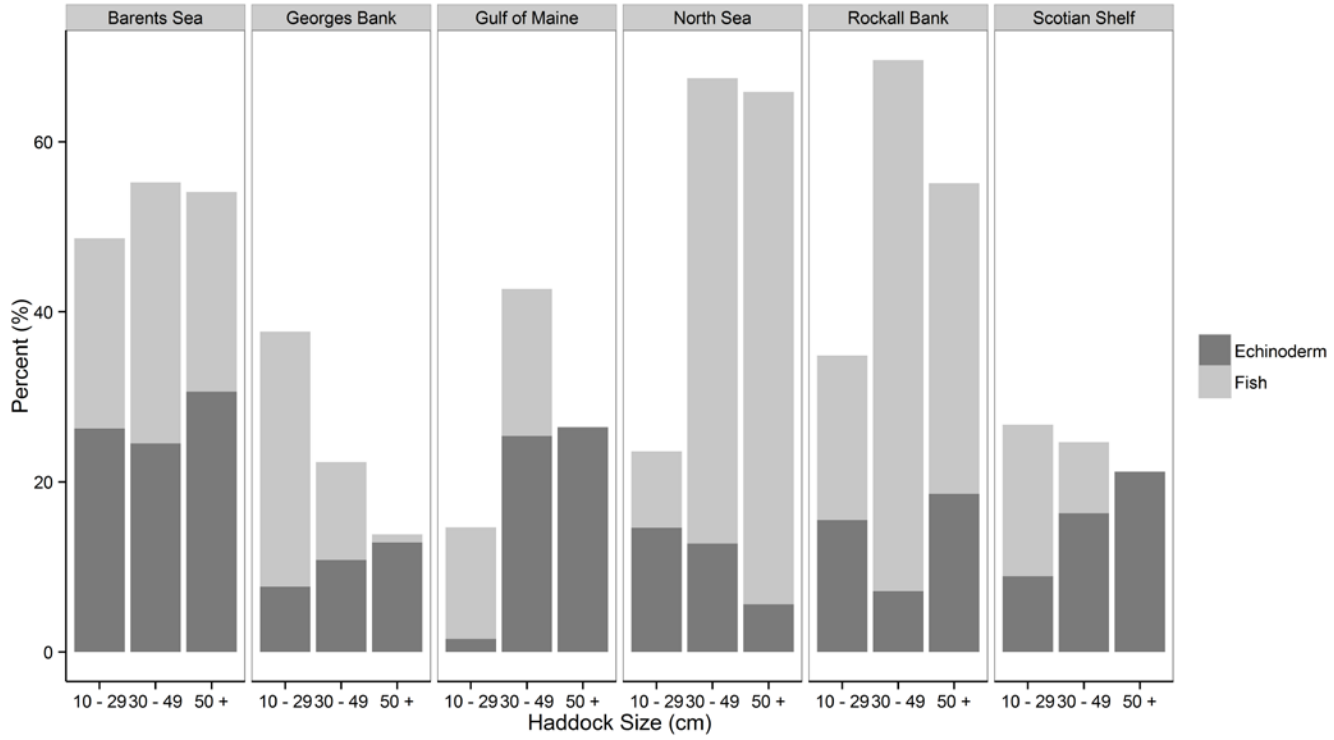


623

624 Figure 3. Diet of different size class of *M. aeglefinus*.

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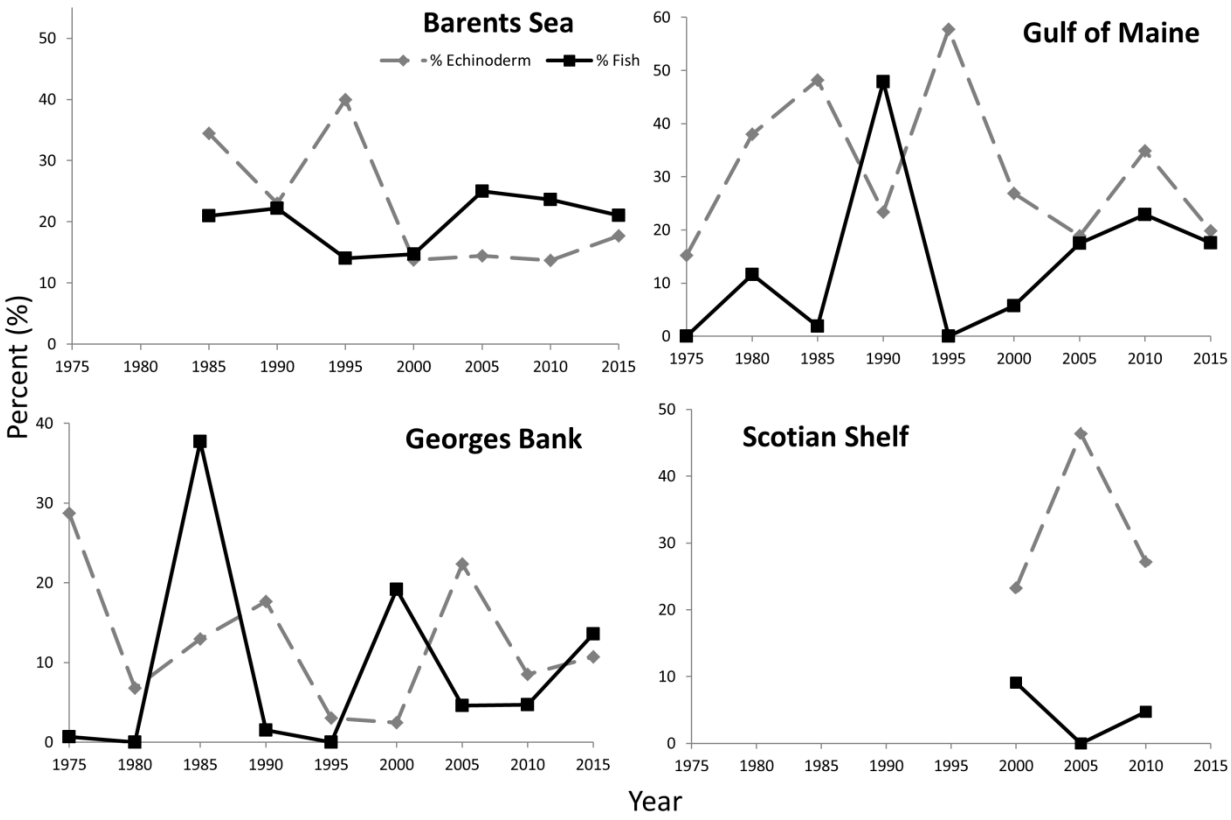


626

627 Figure 4. Diet of *M. aeglefinus* over time.